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Title: Burning savanna for avian species richness and functional diversity

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ABSTRACT

Prescribed fire is used throughout fire-prone landscapes to conserve biodiversity. Current best practice in managing savanna systems advocates methods based on the assumption that increased fire-mediated landscape heterogeneity (pyrodiversity) will promote biodiversity. However, considerable knowledge gaps remain in our understanding of how savanna wildlife responds to the composition and configuration of pyrodiverse landscapes. The effects of pyrodiversity on functional diversity has rarely been quantified and assessing this relationship at a landscape scale which is commensurate with fire management is important for understanding mechanisms underlying ecosystem resilience. Here, we assess the impact of spatiotemporal variation in a long-term fire regime on avian diversity in North West Province, South Africa. We examined the relationship between (a) species richness, (b) three indices of functional diversity (i.e., functional richness, functional evenness and functional dispersion) and four measures of pyrodiversity, the spatial extents of fire age-classes, and habitat type at the landscape-scale. We then used null models to assess differences between observed and expected functional diversity. We found that the proportion of newly-burned (<1-year post-fire), old, unburned (≥10 years post-fire), and woodland habitat on the landscape predicted species and functional richness. Species richness also increased with the degree of edge contrast between patches of varying fire age, while functional dispersion increased with the degree of patch shape complexity. Lower than expected levels of functional richness suggest that habitat filtering is occurring, resulting in functional redundancy across our study sites. We demonstrate that evaluating functional diversity and redundancy is an important component of conservation planning as they may contribute to previously reported fire resilience. Our findings suggest that it is the type and configuration, rather than the diversity, of fire patches on the landscape that promote avian diversity and conserve ecological functions. A management approach is needed that includes significant coverage of adjacent newly-burned and older, unburned savanna habitat; the latter, in particular, is inadequately represented under current burning practices.

KEYWORDS

Avian conservation, functional diversity, fire management, heterogeneity, pyrodiversity, savanna

INTRODUCTION

Savanna is the most fire-prone biome on earth (Chuvieco et al. 2016), with fire acting as an important driver of habitat structure and ecosystem function (Glover 1968). Prescribed burning has been widely used throughout savanna regions, often to enhance grazing opportunities for mammals (by stimulating the sprouting of grasses), whilst also reducing bush encroachment and pre-empting wildfires by reducing fuel loads (Van Wilgen 2009). More recently, however, the focus of fire management has shifted towards burning as a means to conserve—and even promote—biodiversity through fire-mediated landscape heterogeneity (Van Wilgen 2009, Kelly and Brotons 2017).

Prevailing contemporary burning methods are rooted in the ecological theory that increased landscape heterogeneity will result in increased biodiversity (Parr and Brockett 1999). By applying fires that vary in time and space, land managers attempt to achieve some of the patchiness that is inherent to fire prone ecosystems (Brockett et al. 2001). These "patch-mosaic" burning methods are based on the idea that pyrodiversity promotes biodiversity (Martin & Sapsis 1991; Parr & Brockett 1999). Although initial developments of patch-mosaic burning methods were formalized in Pilanesberg National Park and Kruger National Park in South Africa (Brockett et al. 2001), variations of these methods are now employed worldwide, including Australia (Taylor et al. 2012, Sitters et al. 2014), North America (Holcomb et al. 2014) and across southern Africa (Mulqueeny et al. 2010). While the effects of heterogeneous fire regimes on wildlife have mostly been studied in Australia, in shrub and forested habitats (Taylor et al. 2012, Sitters et al. 2014, Farnsworth et al. 2014), relatively few studies have evaluated the pyrodiversity-biodiversity relationship in African savannas (*but see* Davies et al. 2012, Beale et al. 2018). In South Africa, patch-mosaic burning is used in protected areas to achieve conservation goals (Brockett et al. 2001, Van Wilgen 2009) despite limited evidence that these regimes enhance local biodiversity.

Empirical evidence has provided mixed support for the pyrodiversity promotes biodiversity (hereafter PPB) hypothesis (Taylor et al. 2012, Tingley et al. 2016), with recent work demonstrating that this relationship is species-specific (Taylor et al. 2013) and may be contingent on habitat type (e.g. forests; Ponisio et al., 2016; Tingley et al., 2016) or climate (Beale et al., 2018). Varied findings may also result from how studies characterize and quantify both pyrodiversity and biodiversity. Heterogeneity is multifaceted and has temporal and spatial traits characterized by the type, shape and

arrangement of habitat patches, which can affect ecological systems and their functioning (Wiens 2000). However, most studies investigating pyrodiversity have investigated the temporal attribute time-since-fire (Taylor et al. 2012, Haslem et al. 2012) or fire frequency (Davies et al. 2012). A focus on temporal attributes is justifiable because patch-mosaic methods emphasize time-since-fire (Brockett et al. 2001) and temporal attributes may correspond with vegetation succession and structure (Fox 1982). However, few studies have evaluated the impact of the spatial attributes of pyrodiversity (e.g. complexity and configuration) on animal communities (*but see* Sitters et al. 2014), despite the influence of spatial structure on the diversity, composition and persistence of communities in heterogeneous landscapes (Pickett and Cadenasso 1995). Studies have demonstrated that the size, shape (i.e., perimeter to area ratio) and edge density (Herrando et al. 2003), as well as the spatial composition (Sitters et al. 2014) of patches in a landscape mosaic influence species richness, resulting from enhanced resource availability and differentiation.

While species richness remains the most widely used measure of diversity when investigating fauna-fire relationships, there is an emerging consensus on the importance of investigating the response of functional diversity (i.e. the abundance and distribution of species traits that affect ecosystem functions) to disturbance (Laliberté et al. 2010, Lindenmayer et al. 2015). Functional traits such as foraging strategy, dispersal ability, nesting location, and habitat specialization are sensitive to the disturbance-induced changes in vegetation structure that usually accompany fire (Luck et al. 2012). Furthermore, exploring the relationship between environmental heterogeneity and functional diversity can illuminate processes contributing to the formation and maintenance of species assemblages (McGill et al. 2006, Pakeman 2011) and processes driving ecosystem resilience in fire-prone landscapes (Oliver et al. 2015). Resilience—the ability of a community to return to a pre-fire state—has been identified in savanna systems where the response of taxonomic diversity (i.e., species richness) to fire was investigated (Parr and Andersen 2008, Davies et al. 2012, Andersen et al. 2014). Ecosystem resilience depends on functional diversity and how functionally similar species respond to a particular disturbance (Laliberté et al. 2010). Landscape heterogeneity may increase resilience by supporting spill-over and a larger species-pool (Tscharntke et al. 2012) and by providing resources and diverse niches that act as refugia to preserve species and their functions (Oliver et al. 2015). Frequent fires can act as an environmental filter selecting for species with fire-adapted traits, which

has implications for community recovery and long-term ecosystem resilience (Cavender-Bares and Reich 2012). Spasojevic et al., (2016) found that functional diversity in plants—unlike species richness—was a good predictor of community resilience and revealed mechanisms underlying fire resilience at the landscape scale. Understanding functional diversity and ecosystem resilience is vital for conserving biodiversity in fire-prone ecosystems.

Here, we present a study of the effects of fire-mediated heterogeneity on avian taxonomic and functional diversity. We test for relationships between avian diversity and temporal and spatial characteristics of a fire regime at a landscape scale corresponding with the scale of fire prescription. We selected birds as our focal taxon as they are known to respond rapidly to changes in vegetation structure following fire (Barton et al. 2014) and to landscape heterogeneity (Morelli et al. 2013). Furthermore, birds are a diverse group that can be readily assigned to guilds based on traits, such as trophic position and resource requirements, that determine their contribution to different ecological functions. The objective of this study was therefore to test the hypothesis that avian diversity increases with increasing pyrodiversity. We take a multifaceted approach, investigating the effects of multiple spatiotemporal landscape variables on avian species richness and functional diversity.

METHODS

Study Area

The study was conducted at Pilanesberg National Park (hereafter Pilanesberg) and the nearby (5km) Mankwe Wildlife Reserve (hereafter Mankwe) in North West Province, South Africa. Both protected areas primarily comprise semi-arid savanna habitat. Average annual rainfall at Pilanesberg was 637 mm (1999-2016; range 411-993 mm) and at Mankwe was 625 mm (2010–2016; range 352–835 mm), which falls primarily between November and March. The vegetation is classified as sourish mixed bushveld and is a combination of open savanna grasslands and deciduous woodland dominated by *Acacia* and *Combretum* species (Acocks 1988). Most fires occur in winter between May and August and, at both sites, are prescribed by land-managers, with occasional unplanned fires resulting from lightning or anthropogenic causes. At Mankwe a modified rotational block burning regime is used wherein established blocks of savanna habitat are burned every four to five years whilst maintaining some areas that burn more frequently, less frequently or not at all. The fire regime at Pilanesberg is

based on the 'patch-mosaic burning' method and fires are ignited to vary spatially and temporally (Brockett et al. 2001). Both protected areas sit within a matrix of human dominated landscapes and are immediately adjacent to developed areas, residential zones, and agriculture. The realities of this setting require an adaptive fire management regime, with decisions based on wildfire prevention or safety sometimes taking precedence over competing conservation priorities.

Fire history maps were digitized in and around the two study sites using Landsat 5 and 8 surface reflectance imagery from 1989–2016 (30-m resolution). To locate individual fire patches, Landsat data was displayed using the bands red, middle infrared, and near-infrared in blue, green, and red colours (Bowman et al. 2003, Jones et al. 2013). The boundary of every fire (including unburned interior areas) occurring between January 1989 and March 2016 was hand digitized at a constant scale (1:25,000). To verify the dates of ignition derived from Landsat data, we used fire maps provided by the land managers for each study area. Each fire patch was assigned an age-class based on the calendar year in which it burned (see Appendix S1: Figure S1). We produced a generalized vegetation map (30-m resolution) with Landsat 8 surface reflectance imagery of the study region. A supervised maximum-likelihood classification was performed in Quantum GIS (QGIS 2016) to classify habitat into two generalized vegetation classes: closed-canopy tree covered areas (hereafter woodland) and open savanna. The resulting raster was made up of discrete patches of woodland within a matrix of open savanna, with the latter including open savanna and savanna interspersed with shrubs and trees.

Study Design and Landscape Variables

Sampling points were located throughout the study area using a restricted-random sampling method. Points were distributed to capture the range of fire age-classes at both sites and were >250 m apart (See Appendix S1: Figure S1 for the range of fire age-classes and point locations at each site). At Pilanesberg all points were placed within 50-m of a dirt track or road to facilitate access and observer safety. Landscape variables were measured at a 100-ha circular spatial extent (radius of 564 m) centred on each sampling point and were derived from the previously described rasters using Fragstats 4.0 (Mcgarigal et al. 2012). This spatial extent is large enough to capture the range of existing variation for each landscape variable and is relevant to prescribed fire management at both study areas. For example, median fire size at Pilanesberg National Park is approximately 100 ha (Brockett

et al. 2001). Furthermore, 100 ha has been identified as the scale at which birds are responding to landscape-level variation in a fire regime (Burgess and Maron 2016).

We computed six fire variables and one habitat variable (Table 1) within each 100-ha landscape mosaic. To characterize pyrodiversity and components of the fire regime we calculated metrics to describe the composition and configuration of the fire mosaic. The composition of the fire mosaic was explained by the Shannon habitat diversity index (SHDI), which accounts for the number of age-classes in a landscape and their proportional area. SHDI is commonly used to quantify pyrodiversity on the landscape (Kelly et al. 2012, Taylor et al. 2012, Nimmo et al. 2013, Sitters et al. 2014, Farnsworth et al. 2014). The shape and configuration of the mosaic were described using the SHAPE variable in Fragstats, which quantifies the area-weighted mean shape complexity of fire patches within a landscape, weighted by their area (Mcgarigal et al. 2012). We also calculated the area-weighted mean edge-contrast index (ECON), which is a measure of configuration and describes the difference in time-since-fire between adjacent patch types. We assigned contrast values (0–1) to each patch ranked by the degree of contrast between the burn age-class of the patch and that of neighbouring patches, with a value of 0 corresponding to no difference in fire age and a value of 1 being maximum contrast (i.e., maximum contrast edges in our dataset occurred between patches that had not burned in the recorded fire history and patches that burned in the survey year). We calculated the proportion of the landscape that had burned ≥10 years previously (OLD hereafter) and recently burned habitat (burns occurred <1 year prior to the survey, NEW hereafter). We also calculated the area-weighted mean fire frequency (FREQ), which describes the number of times a landscape has burned. We included a variable quantifying the proportion of the landscape that is woodland (WOOD). We did not include a variable for savanna grassland cover as it was effectively the inverse of WOOD. See Table 1 for a detailed description of the landscape variables.

Bird Surveys

Sampling points were surveyed for birds twice during two consecutive sampling seasons (October-March): once at the beginning of the season (October–November 2014 and 2015) and once towards the end of the season (January–March 2015 and 2016), resulting in four surveys per point. Surveys consisted of a 10-minute point count where all birds seen and/or heard within a 100-m radius were

recorded. The observer used a laser rangefinder (Nikon Aculon-500m) to measure the distance to each detected bird. Point counts were conducted by the same experienced observer (TD) during the peak of vocal activity (sunrise until 10 am), and only during good weather conditions without rainfall or strong wind. The time of day that repeat visits to a point occurred was varied to reduce sampling bias. Birds flying-over and not using the habitat or birds associated with water bodies were excluded from analyses. We visited 339 unique point count locations (161 at Pilanesberg and 178 at Mankwe), with 302 of these points surveyed twice in the first season and 331 of these points surveyed twice in the second season (differences owing to access conditions), resulting in 1266 point counts.

Avian Traits and Life History Characteristics

We compiled qualitative and quantitative avian functional traits for all species detected during surveys. Trait data were extracted from Hockey et al. (2004) and comprised traits that may influence a species' interaction with the environment, including life history traits and morphological characteristics. Traits included foraging strategy, foraging substrate, nest site, and habitat breadth, which impact how a species responds to environmental disturbance (Sekercioglu 2006; Luck 2012). For traits that were highly correlated (Pearson correlation coefficient: $r > 0.7$), we retained only the trait considered most likely biologically relevant to our hypotheses; this resulted in 11 functional traits (see Appendix S1: Table S1 for a description of the functional traits). Many morphometric traits are correlated with body mass; we used the ratio of wing length to body mass to represent mass-independent morphology. Where necessary, data were normalised by square root (culmen length) or log- (clutch size and ratio of wing length to body mass) transformation.

Bird Species Richness and Functional Diversity

Bird species richness (hereafter SR)—the number of species recorded at each point—was calculated for each breeding season by compiling the total number of species at each point recorded over the two surveys. Avian functional diversity (hereafter FD) was quantified using the 11 functional traits and species abundances at points to produce a Gower dissimilarity coefficient, using the package 'FD' (Laliberté and Legendre 2010, Laliberté et al. 2014) in program R (R Development Core Team 2016). For each species and each breeding season, we used the maximum count from the

two surveys as our measure of abundance for a point. We estimated three indices of FD for each survey point: 1) functional richness, 2) functional evenness, and 3) functional dispersion. Functional richness represents the multidimensional functional trait space occupied by the community at a survey point (Villéger 2008). Specifically, it is estimated using the convex hull volume of the functional space (Villéger 2008). Functional evenness describes how regularly species abundances are distributed in functional trait space (Laliberté and Legendre 2010). Functional dispersion measures how species are distributed in functional trait space, which is computed by the mean distance of individual species to the centroid of this trait space, weighting these distances by species abundance (Laliberté and Legendre 2010). Functional dispersion is unrelated to species richness and provides an estimate of the degree of functional trait heterogeneity within a community (Laliberté and Legendre 2010). These measures of FD can be estimated from categorical, ordinal or continuous trait data, allow for missing trait data and the weighting of individual traits (Laliberté and Legendre 2010). For traits where an individual species can have more than one attribute (i.e. foraging behaviour), we weighted binary attributes by the reciprocal of the number of attributes for each trait (Laliberté and Legendre 2010).

Statistical Analyses

We used linear mixed models (LMMs) with a Gaussian error to model the relationship between avian diversity (i.e., SR and the three indices of FD) and the explanatory variables (see Table 1). We conducted preliminary data exploration following Zuur, Ieno & Elphick (2010). Before modelling we checked for multi-collinearity among explanatory variables using variance inflation factors (VIF) from the 'car' package in R (Fox and Weisberg 2019). Variables with a VIF > 3 were considered collinear (Zuur et al. 2010). The variable ECON was collinear with OLD ($r = 0.70$, VIF = 4.15); because of this, we did not fit any models that contained both OLD and ECON. Each model contained the variables SITE and YEAR, to account for between site and between year variation. We included survey point as a random effect to account for repeated surveys across sampling seasons while all other variables were treated as fixed effects. Prior to modelling, the response and explanatory variables were scaled ($[x - \bar{x}]/\sigma_x$) to provide standardized coefficients that were comparable among variables.

For each response variable (diversity metrics) we built an *a priori* candidate model set (n = 181), which included models with both additive and interactive combinations of the explanatory variables and a null (intercept only) model. An information theoretic approach to model selection was taken and we ranked models using Akaike's Information Criterion (AICc), which includes a correction for small sample size (Burnham and Anderson 2002). Next, differences between the AICc-best fit model and all other candidate models (ΔAICc) were used to calculate Akaike weights (w_i: the likelihood of a model being the best in the set of candidate models; Burnham and Anderson 2002). These ranked model weights were then summed to create a 95% confidence model set. Models with similar log-likelihood values and less than the ΔAICc of simpler nested models were removed from the confidence set (Richards 2008, Arnold 2010). We model averaged across all models in this confidence set and computed 95% confidence intervals. Predictor variables were deemed to have an influence on the response variable if the 95% confidence intervals of their averaged coefficients did not overlap with zero. Model selection and model averaging were conducted using the 'nlme' (Pinheiro et al., 2014) and 'MuMIn' packages (Barton, 2016) in R (R Development Core Team 2016).

The residuals of the top models (AICc-best fit model for each diversity metric) were examined to confirm that the assumptions of regression were not violated (Bolker et al. 2009). An estimate of the variance explained by models was obtained by computing the marginal R^2 (i.e., fixed effects only) and conditional R^2 (i.e., fixed and random effects) values (Nakagawa and Schielzeth 2013). We also tested for spatial autocorrelation in the residuals of these models using a Moran's I test using the R package 'ape' (Paradis et al. 2004) and spline correlograms (produced with 1000 permutations) using the 'ncf' package (Bjornstad 2016). No marked spatial dependency was observed (Moran's $I < 0.02$; see Appendix S1: Figure S3) minimizing concerns that our results were distorted by pseudoreplication resulting from the proximity of some sampling points; this apparent robustness to overlapping buffers around neighbouring points is consistent with previous findings (Zuckerberg et al. 2012).

We used a null model approach to investigate if changes in FD are driven by changes in SR (Pakeman 2011, Rolo et al. 2016). This approach allows for the comparison of FD between observed communities and randomly assembled communities of equal species richness and is recommended when observed FD is correlated with SR (Swenson 2014). The three indices of FD and SR were independent of one another ($r<0.3$), except for functional richness and SR ($r = 0.72$). We generated

1000 random assemblages at each survey point by maintaining the observed SR and randomly assigning species from the entire observed species pool. Functional richness was then calculated for each simulated community at each survey point in each season. Observed functional richness was considered significantly different from the expected functional richness if it fell outside of the central 950 ranked random values of the null distribution. The magnitude and direction of the deviation of observed functional richness (Obs) from the null model was measured using a standardized effect size (FRic.SES) as FRic.SES = (Obs – Exp_{mean}) / Exp_{sd}, where Exp_{mean} and Exp_{sd} are the mean and the standard deviation of expected functional richness values, respectively (Gotelli and Rohde 2002). Standardized effect sizes can help make inference about community assembly processes (Rolo et al. 2016). The null hypothesis is that the average FRic.SES at each site is equal to zero. Deviations from zero across communities or environmental variables can indicate community assembly processes (Rolo et al. 2016). For example, significantly higher than average FRic.SES values can indicate niche complementarity, in which coexisting species exhibit niche differentiation, while significantly lower than average FRic.SES values can indicate environmental filtering (Kirkpatrick et al. 2018). We fit LMMs, including survey point as a random effect and excluding the intercept, to test whether FRic.SES values significantly deviated from zero.

RESULTS

A total of 32,880 bird records from 213 species were compiled from the surveys over the two sampling seasons. Mean SR across all points was 23.4 (range = 8–50, SD = 6.72). Mean values of FD were: functional richness 0.18 (range = 0.01–0.48, SD = 0.08), functional evenness 0.85 (range = 0.67–0.96, SD = 0.04), and functional dispersion 0.31 (range = 0.09–0.38, SD = 0.03).

RESPONSE OF AVIAN DIVERSITY TO LANDSCAPE VARIABLES

Avian species richness was positively associated with multiple explanatory variables, including the fire variables NEW, OLD and ECON (Figure 1a). Species richness also had a strong positive association with WOOD, indicating that sampling points with a greater proportion of woodland cover surrounding them had higher overall species richness (Figure 1a). The two top ranked models for species richness contained an interaction between NEW and WOOD (Table 2); the effect of NEW on

SR was greater when the landscape contained more woodland (Figure 2a). Functional richness was positively associated with the variables NEW, OLD, and WOOD (Figure 1b). Top models for functional evenness demonstrated low R^2 values (Table 2). However, model averaging revealed that functional evenness was significantly related to the proportion of NEW, but unlike functional richness, the relationship was negative (Figure 1). Functional dispersion was positively associated with the landscape variable SHAPE (Figure 2f). The variables SHDI and FREQ did not have an effect of any of the diversity metrics.

DEVIATION FROM EXPECTED FUNCTIONAL RICHNESS

Values of observed functional richness were positively related to values of species richness (Figure 3). Thus, species rich sites are functionally rich sites. The comparison of observed functional richness to that of simulated communities indicated that the majority (88%) of survey points had lower than expected functional richness and 17% of survey points were significantly lower ($\alpha = 0.05$) than the null distribution (Figure 3). Values of SES.FRic significantly deviated from zero and were consistently negative across the landscape variables (Table 3). The SES.FRic values were lower than expected, given the level of species richness, with the greatest deviations from expected functional richness in the most species rich sites (Figure 4). See Appendix S1: Figure S5 for all relationships between SES.FRic and the landscape variables.

DISCUSSION

In this study, we assessed how bird diversity responded to landscape heterogeneity resulting from nearly three decades of burning. Our findings suggest that taxonomic and functional diversity metrics respond differently to different properties of a fire regime. While we did not find an effect of the composition of the fire regime on avian diversity, we did find an effect of spatial configuration. Moreover, the extent of the extremes of the fire regime, i.e. the amount of newly-burned and old burn areas, best predicted both avian species richness and two measures of functional diversity. We discuss these relationships below, in relation to avian habitat preferences, habitat filtering and functional redundancy, and the implications of fire management practices for conservation.

We have shown that multiple fire and landscape variables influence species richness. Species richness was positively associated with newly-burned habitat, consistent with previous empirical studies of birds (Nkwabi et al. 2011), mammals (Klop and Prins 2008), and other taxa (Moretti et al. 2010). Such associations are recognized as the result of temporary changes in post-fire resources that benefit particular early-successional species (Hutto 1995). However, this association also implies that the influx of post-fire specialists was not matched by an efflux of post-fire evaders, suggesting that many savanna species can tolerate and utilise burned areas. Some species, including disturbance-adapted species, large birds, ground-breeding birds and ground-feeding insectivores preferentially utilize recently burned grassland in South Africa (Bouwman and Hoffman 2007). Many species were far commoner in newly-burned habitat than elsewhere and some species, such as Temminck's courser (*Cursorius temminckii*) and buffy pipit (*Anthus vaalensis*), occurred exclusively in such areas, suggesting that a suite of species rely on annual burns in our study area. The positive relationship between species richness and newly-burned habitat was greater when the landscape contained a greater proportion of woodland cover (Figure 2a). This indicates that locations where new burn and woodland overlap are important for maintaining savanna biodiversity, and is consistent with suggestions that habitat type and vegetation structure are important predictors of how species respond to fire (Barton *et al.* 2014).

We found that species richness was positively related to the extent of old, unburned habitat (≥10 years post-fire), suggesting that late-seral stage vegetation, greater woody cover, and more structurally complex habitats, which are characteristic of long-unburned savanna systems, support more species (Higgins et al. 2007, Levick et al. 2012). Functional richness was also positively associated with the extent of old, unburned savanna; however, the effect of old, unburned areas on functional richness was approximately twice as important as newly burned areas. Late-seral state savanna is characterized by increased vegetation complexity (Higgins et al. 2007), which provides enhanced foraging and nesting opportunities (Barton et al., 2014), ultimately providing greater resources for a range of species and functions. These results correspond with other ecosystems, where the proportion of older, unburned vegetation was deemed an important predictor of avian diversity (Watson et al. 2012, Taylor et al. 2012). Protecting large extents of late-seral habitat is important in many fire-prone systems because unburned sites are important for rare species (Taylor et al. 2012)

and critical resources that support species persistence on the landscape (Haslem et al. 2012). These areas also support processes such as refuge seeking and dispersal (Yarnell et al. 2008) and post-fire recolonization (Watson et al. 2012, Berry et al. 2015), with implications for ecosystem resilience (Nimmo et al. 2015).

The positive relationship between functional richness and newly-burned habitat was unexpected, owing to existing evidence that functional richness declines with increasing disturbances that simplify habitat structure (Laliberté et al. 2010, Pakeman 2011, Edwards et al. 2013). Newly-burned savannas are characterized by bare ground, a simplified herbaceous layer, and early-seral vegetation (Andersen 2003). Yet, because functional richness was correlated with species richness and is sensitive to inflation by rare species with unique traits (Laliberté and Legendre 2010), we attribute the increase in functional richness in newly-burned habitats to an addition of species exploiting post-fire changes in resources and habitat structure (e.g. post-fire specialist and disturbance-adapted species). This addition of species likely also explains the negative relationship between functional evenness and newly burned habitat. Low levels of evenness occur when new species are added to the community and cause greater unevenness in species abundances (Luck et al. 2013). Similarly, a study of Australian birds found that functional diversity responded to recently-burned habitat, including a positive association between this habitat and functional richness (Sitters et al. 2016). This relationship was attributed to the patchy nature of fires, resulting in altered vegetation structure, enhanced fine-scale heterogeneity, and increased resource availability. Similarly, in our system, smaller-scale heterogeneity which is characteristic of African savanna (e.g., from scattered termite mounds or grazing interactions), may contribute to patchy fires that can support a greater range of species and functions (Porensky and Young 2013).

The importance of the proportion of newly burned and unburned habitat suggests that it is the amount of specific habitat types on the landscape, rather than high diversity of habitat types, that predict taxonomic and functional richness. The importance of a few key habitat types suggests that habitat complementation might be occurring where multiple habitat types support the requirements of a species. Habitat complementation—as a driver of species assembly on a heterogeneous landscape—is supported by the positive relationship between species richness and the edge-contrast index. Habitat complementation occurs when the proximity of different habitats allows a species to successfully

exploit them (Dunning et al. 1992). Species may depend on complementary habitats when both habitats provide different but essential resources, such as the hoopoe (*Upupa epops*) that requires complementation between adjacent breeding and foraging habitats (Barbaro et al. 2007). The presence of species that exploit resources in edge ecotones, such as unique vegetation structure found in high-contrast edges (Melin et al. 2018), may also be contributing to the positive relationship between species richness and edge contrast. Some species may prefer edges on a burned landscape if they provide unique or abundant resources; however, very little is known about burn-edge resource selection in birds (Parkins et al. 2018). While, edge-contrast had a positive influence on species richness, it did not influence functional richness. This suggests that the suite of species requiring habitat complementation or exploiting high-contrast edges overlap functionally. Further research to investigate resource use by avian species in edge zones within a burned landscape is needed.

Functional dispersion was positively associated with the shape complexity index. Unlike functional richness, functional dispersion is not influenced by species richness but is influenced by species abundance (Laliberté et al. 2010). Hence, this relationship indicates that landscapes with irregularly shaped burn patches contained functionally unique traits with similar abundances. Similarly, Barbaro *et al.* (2014) identified a positive relationship between landscape diversity in fragmented forests and functional dispersion. As heterogeneous habitats offer an increased number of niches, we expected to find enhanced functional dispersion associated with pyrodiversity (Tscharntke et al. 2012). Previous studies have demonstrated that an increase in functional dispersion promotes ecosystem resilience in fire- and disturbance-prone ecosystems due to an increase in species with diverse functions and disturbance response strategies (Laliberté et al. 2010, Spasojevic et al. 2016). Our results suggest that land managers could achieve more resilient ecosystems with more functionally unique traits by increasing the complexity of fire patch shapes (i.e., perimeter to area ratio). However, as this is one of the first studies to investigate components of avian functional diversity and pyrodiversity, we do not know if this relationship is a common trend in fire-prone landscapes. Further research investigating the relationships between multiple metrics of functional diversity, spatiotemporal fire indices and ecosystem resilience will help to identify general rules to guide conservation management.

The positive relationship between functional richness and species richness reveals that functional richness is largely driven by changes in species richness. This relationship is expected because a larger number of species will fill a larger functional trait space (Villéger 2008). However, most of our sites had avian assemblages that occupied less functional trait space than would be expected due to chance, indicating considerable functional redundancy. This general decrease in trait space was observed across study sites and landscape variables (Appendix S1: Figure S4 & Figure S5) and suggests that habitat filtering is occurring (Cornwell et al. 2006). Habitat filtering occurs when ecological conditions select for species that have similar traits (i.e., a reduction in functional richness) that are suitable for a given site (Cornwell et al. 2006), resulting in the non-random co-occurrence of species that are functionally redundant (Laliberté et al. 2010). It is plausible that a fire-prone environment like our study area, with relatively frequent fires occurring across an ever-changing burn mosaic, has, over time, excluded species lacking fire-adapted traits. In fact, the difference between the observed and expected functional richness was greatest in the most frequently burned sites (Appendix S1: Figure S5).

Functional redundancy has been identified as an important factor affecting resilience and stability in response to disturbance (Luck et al. 2013). Studies have noted that the biota in fire-prone landscapes such as savanna (Parr & Andersen, 2008; Andersen et al., 2014) and Mediterranean woodland (Jacquet & Prodon, 2009) can demonstrate a remarkable degree of resilience to burning. Functional redundancy within a community leads to resilience against the loss of ecosystem functions when species with overlapping traits and ecosystem functions respond differently to environmental stressors or disturbance (Laliberté et al. 2010). However, a better understanding of the contribution of functional redundancy to ecosystem resilience in birds will require knowledge of how particular traits respond to fire. While fire adapted and response traits have been well explored in plants, our understanding of such traits in animals remains limited (Pausas and Parr 2018). Furthermore, it is important that confidence in redundancy to conserve ecological functions does not neglect the importance of rare traits and their contributions to ecological functions. Understanding the mechanisms contributing to ecosystem resilience may assist in identifying thresholds and regime shifts beyond which savanna systems may not return to pre-fire states (Spasojevic et al. 2016).

Pilanesberg had consistently higher species richness across survey points, which is likely due to the presence of several species that occur at this site but do not occur at Mankwe. For some species, like the kori bustard (*Ardeotis kori*), this is likely due to differences in the size of these protected areas. However, despite species differences, we did not observe an effect of site on any measure of functional diversity, indicating that functions are conserved across these two sites. Differences in species richness between years can be attributed to the presence of greater numbers of nomadic or semi-nomadic species we observed in the first survey season following above average rainfall the previous year. Such species included wattled starling (*Creatophora cinerea*), monotonous lark (*Mirafra passerine*) and African quailfinch (*Ortygospiza atricollis*). The addition of these species had a positive effect on functional richness and a negative effect on functional evenness, suggesting that these species are functionally unique. Rare or functionally unique species can provide disproportionate contributions to ecosystem functioning (Bracken and Low 2012, Seymour et al. 2015). Given spatio-temporal variation in the abundance of rare species and their vulnerability to environmental change (Reside et al. 2016), it is important that we understand how functionally unique species (and traits) respond to fire regimes. Such an understanding is critical to provide insights into mechanisms that support ecosystem function and to support the development of management strategies in the face of changing climate and fire regimes (Pausas and Parr 2018).

CONCLUSIONS

Although savanna is the most fire prone habitat on earth (Chuvieco et al. 2016), few studies have evaluated the effects of pyrodiversity on savanna fauna (Beale et al. 2018). Moreover, burning regimes (e.g., patch-mosaic burning) that aim to maximize pyrodiversity are among the predominant burning methods in South Africa and elsewhere (Brockett et al. 2001). In this unique study, we demonstrated that high contrast mosaics with good coverage of newly burned and unburned habitat are particularly important for avian diversity. Furthermore, we found that functional diversity was positively related to the spatial complexity of the mosaic, revealing the importance of the configuration of fire mosaics. Yet, care must be taken when implementing a heterogeneous fire regime. Studies have shown that heterogeneous fire mosaics may not protect late-seral habitat (Taylor et al. 2012), leading to the regional extinction of avian species (Brown et al. 2009). The fire regime at

Pilanesberg National Park has resulted in the limited extent of late-seral savanna, suggesting that patch-mosaic burning methods inadequately protect this habitat. Therefore, land managers may have to find a balance between new fire prescriptions, maintaining unburned savanna and mitigating wildfire risk due to increased fuel loads. This challenge is compounded by a changing South African climate where wildfires are predicted to increase in size and frequency (Archibald 2016). These conditions may necessitate an adaptive approach to burning and wildfire prevention, possibly requiring the careful use of infrastructure such as fire-breaks and roads. Our study focused on birds only, but the maintenance of early- and late-seral state as well as intermediate stages of savanna will likely support the habitat requirements of a range of taxa; empirical data—particularly functional data—for other taxa would further contribute to the development of effective fire management strategies for savanna systems. Nevertheless, our study suggests that fire regimes that protect late seral habitats adjacent to newly burned habitats and enhance the spatial configuration of fire patches will conserve savanna species and their functions.

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Data Availability

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.z612jm68b

Table 1. Explanatory variables used to characterize the landscape.

Variable	Description	Abbreviation	Range
Fire Age-Class Diversity*	Shannon's diversity index measures landscape diversity by the number of patch types (fire age classes) and the proportional area distribution among patch types in a 100-ha landscape.	SHDI	0.00–2.03
Fire Shape Complexity*	Area-weighted mean shape index measures the complexity of patch shapes in a 100-ha landscape. Patch shape is compared to a square of the same size with a square having the minimum value of one.	SHAPE	1.14–2.29
Edge Contrast Index*	Area-weighted mean edge contrast index quantifies the average edge contrast for all patches in a 100-ha landscape. Each segment of a patch's perimeter is weighted by the degree of contrast in fire age of the adjacent patch. High index values mean that the edge is of high contrast.	ECON	0.00–49.53
Fire frequency	Area-weighted mean of the fire frequencies (number of times a pixel has burned since 1989) in a 100-ha landscape.	FREQ	0.09–15.01
New Habitat	Proportion of a 100-ha landscape that was recently burned (<1 year).	NEW	0.00–1.00
Old Habitat	Proportion of a 100-ha landscape that has not burned in ≥10 years	OLD	0.00–0.97
Woodland Habitat	Proportion of a 100-ha landscape that is tree covered	WOOD	0.00–1.00
Site	Pilanesberg National Park or Mankwe Wildlife Reserve	SITE	
Year	Sampling season 1 or 2	YEAR	

*For a more detailed description of these variables see Mcgarigal, Cushman & Ene (2012).

Table 2. Linear mixed models in the 95% confidence set used for model averaging describing the relationship between the four response variables (i.e. species richness, functional richness, functional evenness and functional dispersion) and the explanatory variables. Explanatory variables are described in Table 1. In addition to the explanatory variables listed for each model, all models included the fixed effects 'site' and 'year' and the random effect 'survey point'. The log-likelihood values are indicated by logL; k denotes the number of parameters in each model; ΔAIC_c is the difference in the Akaike's Information Criterion (AIC_c) values between a model and the model of best fit; and *w* is the Akaike weight which represents the weight of evidence in support of a model. The marginal R^2 (R^2_m) is the variance explained by the fixed factors and the conditional R^2 (R^2_c) is the variance explained by the fixed and random factors.

Model	*log*L	*k*	ΔAIC_c	*w*	R^2_m	R^2_c
Species Richness						
OLD + NEW *WOOD	−765.04	9	0.00	0.23	0.27	0.60
ECON + NEW*WOOD	−765.08	9	0.09	0.22	0.27	0.60
NEW + OLD*WOOD	−765.11	9	0.15	0.21	0.27	0.60
NEW + OLD + WOOD	−766.75	8	1.36	0.12	0.26	0.60
NEW + ECON + WOOD	−766.94	8	1.75	0.10	0.26	0.60
SHDI + NEW *WOOD	−767.06	9	4.05	0.03	0.26	0.60
NEW *WOOD	−768.36	8	4.60	0.02	0.25	0.61
NEW + WOOD + SHDI	−768.87	8	5.62	0.01	0.25	0.60
NEW + WOOD	−770.39	7	6.60	0.01	0.25	0.60
ECON + WOOD + FREQ	−769.58	8	7.03	0.01	0.26	0.59
Functional Richness						
NEW + OLD + WOOD + SHAPE	−854.02	9	0.00	0.39	0.12	0.22
NEW + OLD + WOOD	−855.23	8	0.36	0.32	0.12	0.23
OLD + WOOD + SHAPE + FREQ	−855.57	9	3.11	0.08	0.12	0.22
OLD + WOOD + SHAPE	−856.87	8	3.65	0.06	0.12	0.22
OLD + WOOD + FREQ	−856.96	8	3.83	0.06	0.12	0.23
Functional Evenness						
NEW + ECON + WOOD	−885.28	8	0.00	0.26	0.02	0.02
NEW + ECON	−886.32	7	0.03	0.26	0.02	0.02
NEW + WOOD	−886.42	7	0.24	0.23	0.02	0.02
NEW	−887.94	6	1.22	0.14	0.02	0.02
ECON	−889.10	6	3.55	0.04	0.02	0.02
Functional Dispersion						

Model	*log*L	*k*	ΔAIC_c	*w*	R^2_m	R^2_c
ECON + SHDI + SHAPE	−842.75	8	0.00	0.36	0.09	0.09
SHAPE	−844.83	6	0.06	0.35	0.09	0.09
ECON + FREQ	−844.88	7	2.20	0.12	0.09	0.09
ECON	−845.91	6	2.22	0.12	0.08	0.09

Table 3. Variation in functional richness standardized effect sizes (FRic.SES ± SE) and *P*-values with the landscape variables and species richness as compared to a null model

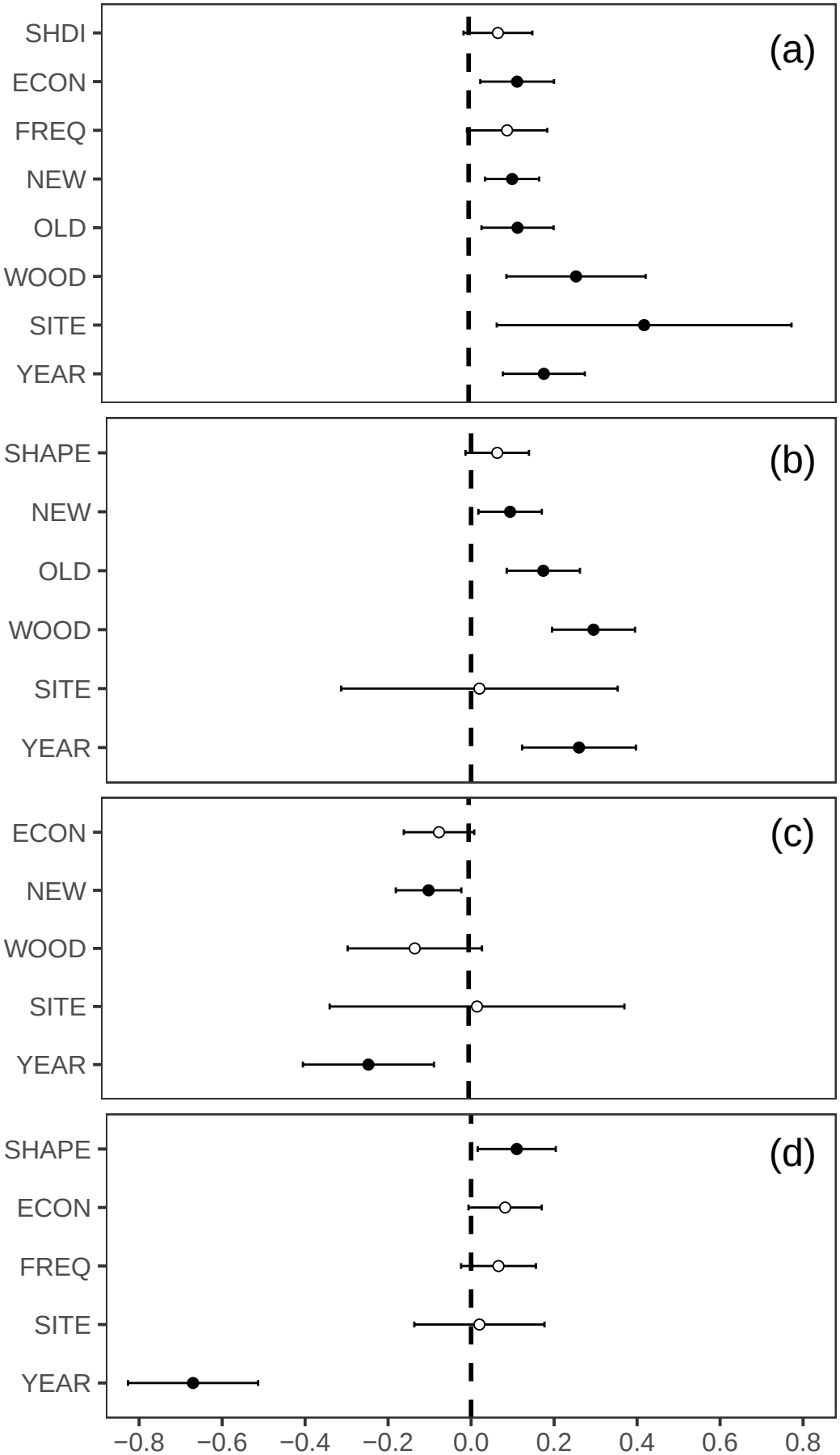
	FRic.SES	*P*-value
Fire age-class diversity (SHDI)	−1.01 ± 0.06	<0.001
Fire age-class diversity (SHDI)	−0.66 ± 0.03	<0.001
Edge contrast index (ECON)	−0.06 ± 0.005	<0.001
Fire frequency (FREQ)	−1.14 ± 0.005	<0.001
Proportion of recently burned habitat (NEW)	−1.41 ± 0.16	<0.001
Proportion of unburned habitat (OLD)	−1.42 ± 0.32	<0.001
Proportion of woodland habitat (WOOD)	−1.82 ± 0.10	<0.001
Species richness	−0.05 ± 0.001	<0.001

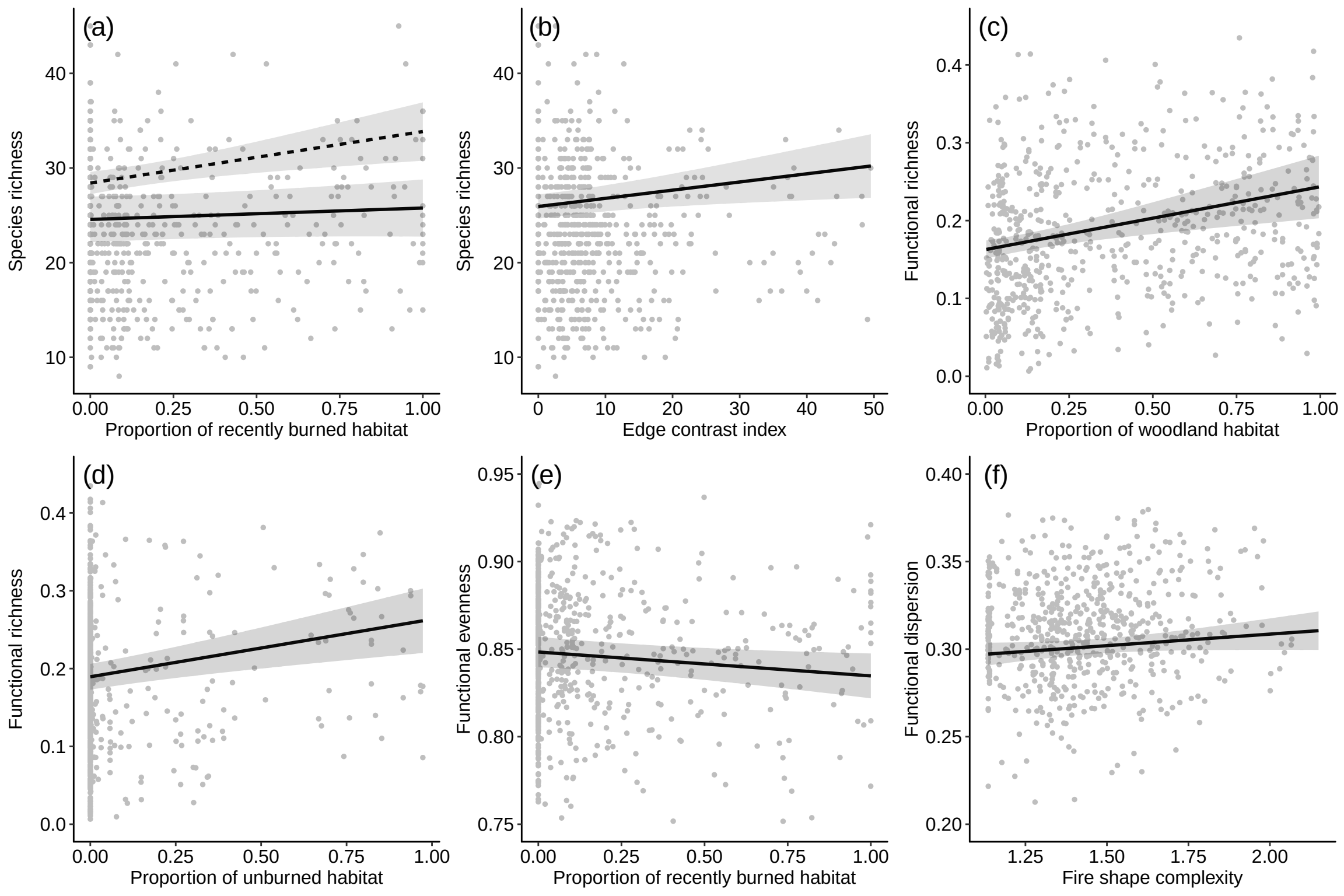
Figure 1. Standardized model-averaged parameter estimates and 95% confidence intervals; effects of each predictor variable (for definition see Table 1) on (a) species richness, (b) functional richness, (c) functional evenness and (d) functional dispersion in 100-ha landscapes in semi-arid South Africa. Solid circles represent variables for which 95% CI does not overlap zero. Absent predictor variables represent a parameter that was not included in the top model set for model averaging.

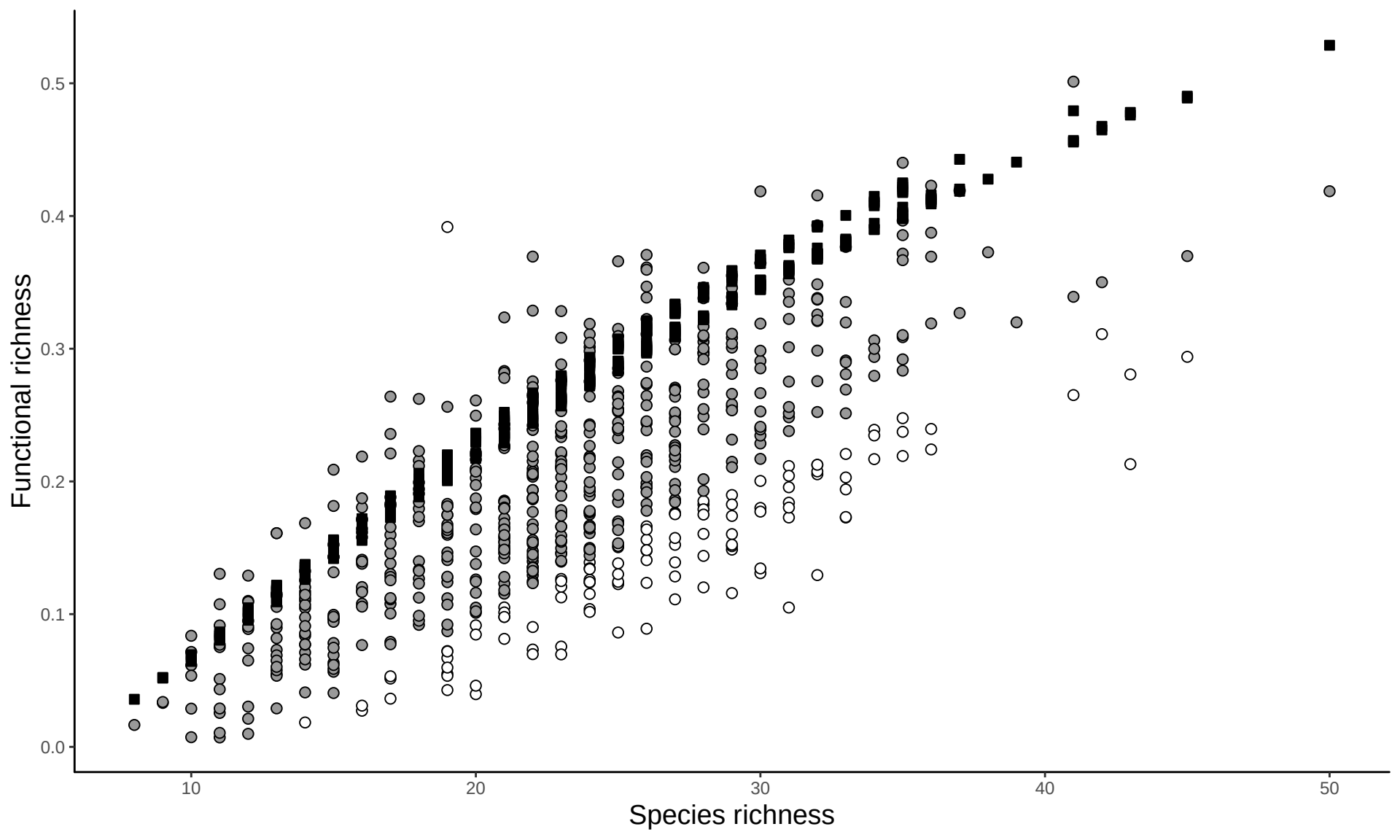
Figure 2. The relationship between avian diversity and key landscape variables. Models are shown for species richness (a, b), functional richness (c, d), functional evenness (e), and functional dispersion (f). Shading represents the 95% confidence intervals. In (a) modelled avian species richness is shown in relation to the proportion of newly-burned habitat, in areas of low (solid line) and high (dashed line) woodland cover. Low woodland cover is represented in these models as the 10^{th} percentile of recorded woodland cover and high woodland cover as the 90^{th} percentile.

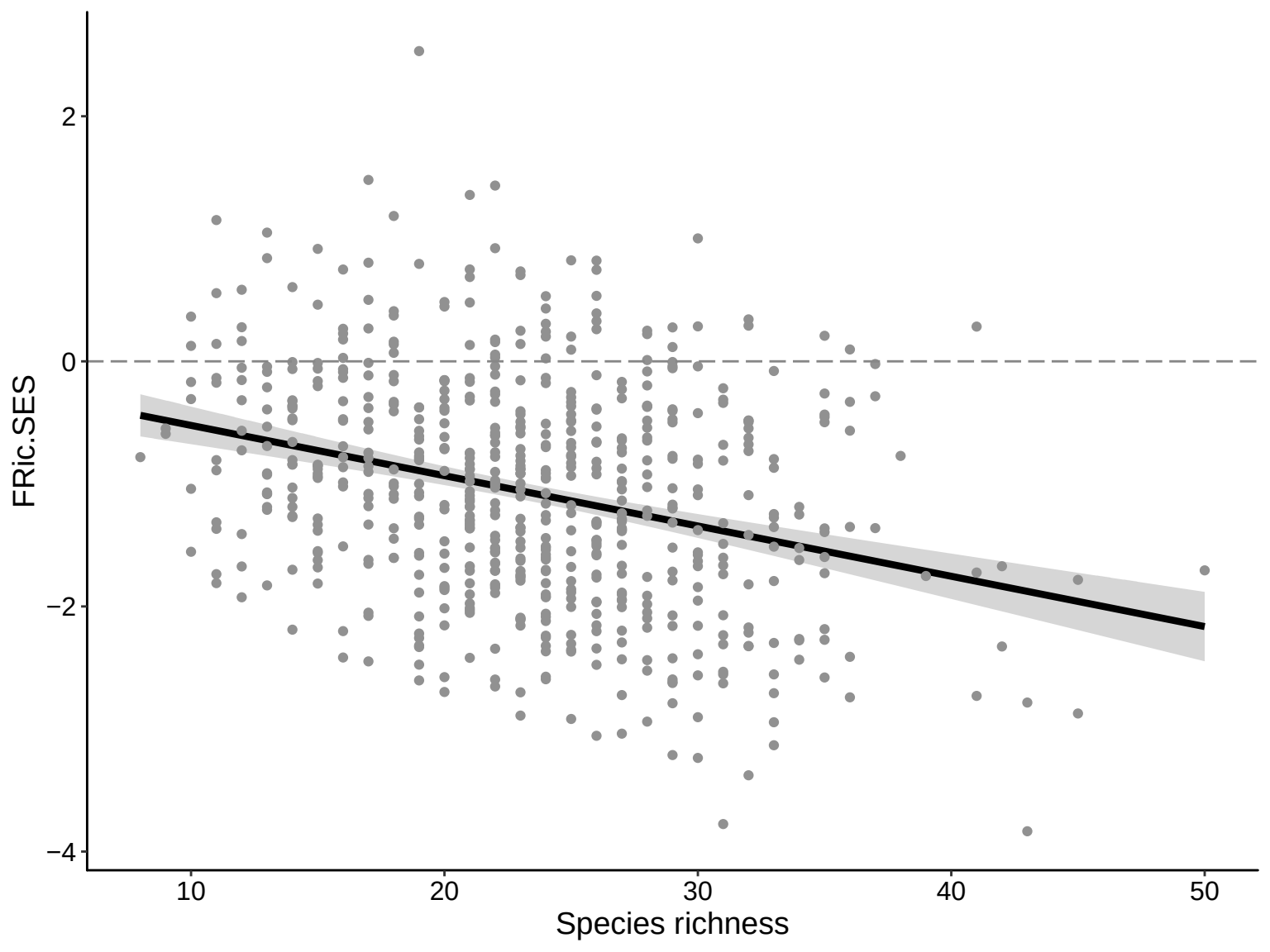
Figure 3. The observed (circles) and expected (black squares) functional richness values against the observed species richness. Open circles denote communities for which the observed functional richness differed significantly ($\alpha = 0.05$) from expected at a given level of species richness.

Figure 4. The relationship (solid line) and 95% confidence intervals (shaded area) between FRic.SES and observed species richness from a linear mixed model.


SHDI
ECON
FREQ
NEW
OLD
WOOD
SITE
YEAR
(a)
SHAPE
NEW
OLD
WOOD
SITE
YEAR
(b)
ECON
NEW
WOOD
SITE
YEAR
(c)
SHAPE
ECON
FREQ
SITE
YEAR
(d)
−0.8
−0.6
−0.4
−0.2
0.0
0.2
0.4
0.6
0.8


(a)
Species richness
Proportion of recently burned habitat
(b)
Species richness
Edge contrast index
(c)
Functional richness
Proportion of woodland habitat
(d)
Functional richness
Proportion of unburned habitat
(e)
Functional evenness
Proportion of recently burned habitat
(f)
Functional dispersion
Fire shape complexity


Functional richness
0.0
0.1
0.2
0.3
0.4
0.5
10
20
30
40
50
Species richness


FRic.SES
2
0
−2
−4
10
20
30
40
50
Species richness